GOLDEN-WINGED WARBLERS (*VERMIVORA CHRYSOPTERA*) OF THE SOUTHERN APPALACHIANS: BEHAVIOR, ECOLOGY, AND CONSERVATION OF A DECLINING NEOTROPICAL MIGRANT SONGBIRD

A thesis presented to the faculty of the Graduate School of Western Carolina University in partial fulfillment of the requirements for the degree of Master of Science in Biology.

By

Jamie Amanda Harrelson

Director: Dr. Jeremy Hyman
Associate Professor of Biology
Biology Department

Committee Members: Dr. Barbara Ballentine, Biology
Dr. Kathy Mathews, Biology

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ABSTRACT

GOLDEN-WINGED WARBLERS (*VERMIVORA CHRYSOPTERA*) OF THE SOUTHERN APPALACHIANS: BEHAVIOR, ECOLOGY, AND CONSERVATION OF A DECLINING NEOTROPICAL MIGRANT SONGBIRD

Jamie Amanda Harrelson, M.S.

Western Carolina University (June 2015)

Director: Dr. Jeremy Hyman

Research on the Golden-winged Warbler (*Vermivora chrysoptera*), a Neotropical migrant songbird that has experienced steady population declines over the past forty years, has generally focused on determining habitat requirements for the species, as well as best management practices for creating and maintaining habitat on the birds' breeding grounds. Few studies have investigated behavioral aspects of Golden-winged Warbler (GWWA) biology and few have been conducted in western North Carolina (WNC). For this research project, I sought to map GWWA territories in WNC and measure vegetation characteristics within those territories, as well as conduct a study of male aggression using conspecific playback. The primary goal of the research was to determine whether correlations exist between male aggression and territory/habitat characteristics. I augmented in-the-field vegetation measurements with analysis of LiDAR data on shrub and canopy layers. Sizes of mapped territories were comparable to those found by other researchers. Within-territory vegetation characteristics, such as percent canopy cover, tree basal area, and shrub height, were consistent with results found by other researchers. Overall, results of LiDAR data analysis were somewhat consistent with measurements made in the field. Aggression trial results demonstrated that males exhibited varying responses to playback. This

intraspecific variation may be due to personality traits that remain consistent over a bird's lifetime and/or to the timing of aggression trials with respect to breeding stage. No correlation was found between density of males in a given area and aggression of males defending territories in that area. However, few sites used in this study had more than one male GWWA present; thus, investigations involving male density are not necessarily meaningful. Significant correlations were found between male aggression and tree dbh, shrub density, and shrub height, with tree dbh positively predicting male aggressive response and both shrub density and shrub height negatively predicting aggression. Due to the fact that the sample size of this study was rather small, further research is needed to clarify relationships between male aggression, population density, and habitat characteristics. If correlations between aggression and both body size and reproductive output found in other avian species also apply to GWWA, studies of male GWWA aggression potentially have implications for conservation of the species.

INTRODUCTION

The Golden-winged Warbler (*Vermivora chrysoptera*) is a Neotropical migrant songbird with a breeding range extending from the southern Appalachian Mountains into southern Canada and west into the Great Lakes region (Confer et al. 2011). Its wintering range lies in Central America and northern South America (Confer et al. 2011). Although Golden-winged Warblers (GWWA) occasionally breed in the mountains of northern Georgia (Confer et al. 2011; Klaus 2004), western North Carolina is the most reliable area in which to find nesting individuals within the southern portion of their range.

Golden-winged Warbler populations have experienced drastic declines over the past four decades (Roth et al. 2012). According to data from the US Geological Survey's Breeding Bird Survey, the US population declined approximately 2.6% annually over the period from 1966 to 2011 (Sauer et al. 2014). Habitat loss on the breeding grounds has been one of the primary drivers of the declines; these losses are due to human development and to the fact that many of the early successional habitats used by the species have matured into later successional stages (i.e., forests) and no longer support populations of GWWA (Roth et al. 2012). Hybridization with the Blue-winged Warbler (*Vermivora cyanoptera*) has also contributed to GWWA declines as the breeding range of Blue-winged Warbler has expanded (Confer et al. 2011). Other factors that likely have affected GWWA populations include loss of wintering habitat and brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) (Confer et al. 2011). The species is currently under review for possible listing by the US Fish and Wildlife Service under the Endangered Species Act (USFWS 2013).

Population declines of GWWA in North Carolina prompted the North Carolina Wildlife Resources Commission to designate the species as "Significantly Rare" in its 2005 Wildlife Action Plan (NCWRC 2005). The 2015 Plan revision states that increased management and direct actions to create and maintain habitat are required to restore populations in the state (NCWRC 2014). According to Roth et al. (2012), GWWA breeding in the Appalachian Mountains region account for only 5% of the entire breeding population. Population declines in the region appear to be occurring at faster rates than in the Great Lakes area; thus, GWWA conservation actions in western North Carolina and surrounding areas are critical to forestalling future severe declines of the species (Roth et al. 2012).

GWWA breed in habitats characterized by shrubs and herbaceous plants and territories are often located near a forested edge (Confer et al. 2011). Klaus and Buehler (2001) studied GWWA breeding sites in Nantahala and Cherokee National Forests (North Carolina and Tennessee); they found that GWWA territories were located in areas characterized by young trees (generally less than 15 years old), extensive herbaceous cover, and reduced canopy cover. Additionally, breeding habitats were dominated by hardwood tree species. In these study areas, approximately 77% of GWWA nests successfully fledged young—considerably higher than nest success rates found in a study on GWWA in New York, where only 39% of nests fledged at least one juvenile (JL Confer, unpublished data). Klaus and Buehler (2001) suggested that the habitat found within their study sites was of high quality and that maintenance of the habitat characteristics mentioned previously is generally not achievable without active management in the form of disturbance by fire, logging, or other forms of mechanical control.

Previous research has shown that GWWA tend to be habitat specialists, seeking out particular microhabitat characteristics (Chandler and King 2011). Patton et al. (2010), studying

GWWA in Kentucky, highlighted the importance of forest edges and the accompanying “microclimate features” of such habitats. Proximity to a mature forest edge may have multiple implications for breeding GWWA, such as increased access to nesting materials (Patton et al. 2010) and to canopy trees that provide perches from which males may sing to attract females (Rossell 2001). Given that GWWA tend to forage in the upper branches of trees (Confer et al. 2011), forested edges may serve as particularly good foraging habitat, as well as protective cover, for adult and recently fledged GWWA.

In addition to proximity to forested edges, patchy vegetation has been shown to be an important component of GWWA territories. Rossell et al. (2003) studied GWWA in a western North Carolina wetland and found that the birds preferred to breed in patchy habitats. As GWWA generally nest on or near the ground (Confer et al. 2011), the presence of dense shrub cover near the nest may improve nesting success. Predation of artificial nests located on the ground has been shown to be lower in areas with dense shrub cover (Greenberg et al. 2002) and a dense shrub layer has the potential to negatively impact mobility of some nest predators (Schranck 1972). Thus, the preference for breeding habitat containing patches of shrubs may be related to selection of territories in which predation is minimized (Rossell et al. 2003).

Perhaps equally as important to breeding GWWA as territory- and patch-level characteristics are landscape-level attributes. According to Roth et al. (2012), elevation, amount of forest cover, and dominant plant communities influence appropriateness of habitat for breeding GWWA. In the southern Appalachians, habitats occurring above 610 m and consisting of 50-75% deciduous forest—dominated by, e.g., yellow poplar (*Liriodendron tulipifera*), sugar maple (*Acer saccharum*), and/or oak (*Quercus*) species—should be prioritized for GWWA habitat management (Roth et al. 2012).

Most, if not all, of the published studies on habitat characteristics of GWWA breeding areas have used in-the-field measurements to quantify variables such as canopy cover and shrub cover. Development of Light Detection and Ranging (LiDAR) data acquisition techniques has facilitated investigations of vegetation characteristics on a larger scale. According to USGS (2012), LiDAR, a type of remote sensing, generates three-dimensional models of the surface of the earth via the transmission of laser pulses from an airplane. The amount of time elapsed between transmission of the pulses and receipt of the reflected light is measured by on-board instrumentation. These values are then used to determine the position of objects on the ground; a cloud of points is generated that represents the surface of the earth and objects on it. The quality of laser pulses reflected off of objects can be used to differentiate between various attributes of the landscape (e.g., forest versus impervious surface) (USGS 2012).

LiDAR technology has been utilized for myriad applications including wetland inventories (e.g., Kloiber et al. 2015) and determination of fire effects on forests (e.g., Kane et al. 2014). A recent study by Weisberg et al. (2014) used LiDAR analysis techniques to determine heterogeneity of breeding habitats for birds. For my study, I sought to compare habitat measurements made in the field with those obtained through analysis of LiDAR data. Additionally, use of LiDAR data facilitated analysis of habitat characteristics on a scale larger than that directly measured in the field; thus, LiDAR analysis was used to augment direct measurements.

While patterns of habitat suitability have a significant effect on distribution of breeding birds, avian behavior, including male aggression, also potentially acts to sort individuals across the landscape. Research on Western Bluebirds (*Sialia mexicana*) has shown that breeding ground disputes between more aggressive and less aggressive males often result in the sorting of males into various habitats (Duckworth 2006). Duckworth showed that the most aggressive males were able to outcompete their less aggressive counterparts for the highest quality territories—i.e., those containing the highest density of sought-after nest boxes (2006). Both habitat quality and behavior influence an individual's overall reproductive success. Scales et al. (2013) found that male aggression in Song Sparrows (*Melospiza melodia*) was correlated with larger clutch sizes, which was treated as an indicator of territory quality. The implication of these studies is that males demonstrating more aggression toward conspecifics may be able to obtain higher quality territories and may have higher reproductive success.

I am unaware of any published studies on male GWWA aggression or on potential correlations between aggressive behavior and habitat quality. Male GWWA in search of breeding ground territories likely seek out particular habitat characteristics—i.e., potential indicators of habitat quality—within a larger framework of overall patchiness. Vegetation characteristics, such as amount of herbaceous, shrub, and canopy cover, certainly vary across GWWA territories and those variations may indicate differing levels of territory quality. In this study, I investigated whether male aggression is associated with habitat characteristics that may indicate territory quality.

Habitat quality has the potential to influence the distribution of individuals that likely differ in behavioral characteristics. Likewise, the population density of a species in a particular area often has behavioral and/or reproductive implications. Aggression of males living adjacent to conspecifics may vary depending on the density of individuals in the area. Yoon et al. (2012) studied Orange-crowned Warblers (*Oreothlypis celata*) in Alaska and Canada and found that, in areas with higher population densities, male aggression toward other males of the same species was more pronounced than in habitats with lower population densities. No known studies have investigated correlations between male GWWA aggression and population density.

In the current study, I sought to characterize GWWA territories in the southern Appalachians and conduct behavioral research on the males defending those territories. Specifically, the study included the following objectives: (1) map male GWWA territories and determine territory sizes and male densities; (2) assess vegetation characteristics (e.g., canopy cover and shrub cover) within those territories by conducting in-the-field measurements; (3) compare results for variables measured in the field with those obtained from analysis of LiDAR data; (4) quantify aggression of individual male GWWA; and (5) test for possible correlations between aggression of individual males and measures of territory attributes, including territory size and vegetation characteristics.

This study is significant in that it was conducted in areas in which previous research on GWWA has been limited or nonexistent. To my knowledge, only three of the six sites included in this study had been systematically surveyed for GWWA prior to the start of this project. The study generated communication between GWWA conservation partners (e.g., Audubon North Carolina and the Natural Resources Conservation Service) and private landowners regarding conservation measures that provide and maintain habitat for breeding GWWA. Finally, the research and resulting conclusions will augment previous work in which analysis of GWWA behavior has been largely absent.

METHODS

Field work for the project was conducted between April and August 2014. Survey data from Audubon North Carolina and federal and state agencies, e.g., the North Carolina Wildlife Resources Commission, were used to determine sites at which GWWA were likely to breed in 2014. In late March (i.e., prior to the start of field work), I visited potential study sites to ascertain whether patch-level and landscape-level characteristics were consistent with those preferred by GWWA. I monitored records of bird sightings through eBird and regional listservs to determine the arrival date of GWWA in western North Carolina. I independently conducted all field work for the project.

Study Sites

Six study sites, located in Graham, Haywood, and Jackson counties, were used for the project (Fig. 1). Four sites were located on private land and the other two were in Nantahala National Forest. Private landowners or their liaisons granted permission for land access. Permission was granted by the USDA Forest Service to conduct research in Nantahala National Forest (Special Use Permit number NAN504001).

Sites were chosen based on their accessibility and on the feasibility of mapping territories in areas with more than one male GWWA on territory because (1) the time frame during which breeding Neotropical migrant songbirds are actively defending territories is somewhat narrow, (2) sites with breeding GWWA were spread out over several counties, and (3) I lacked the resources to band individual birds.

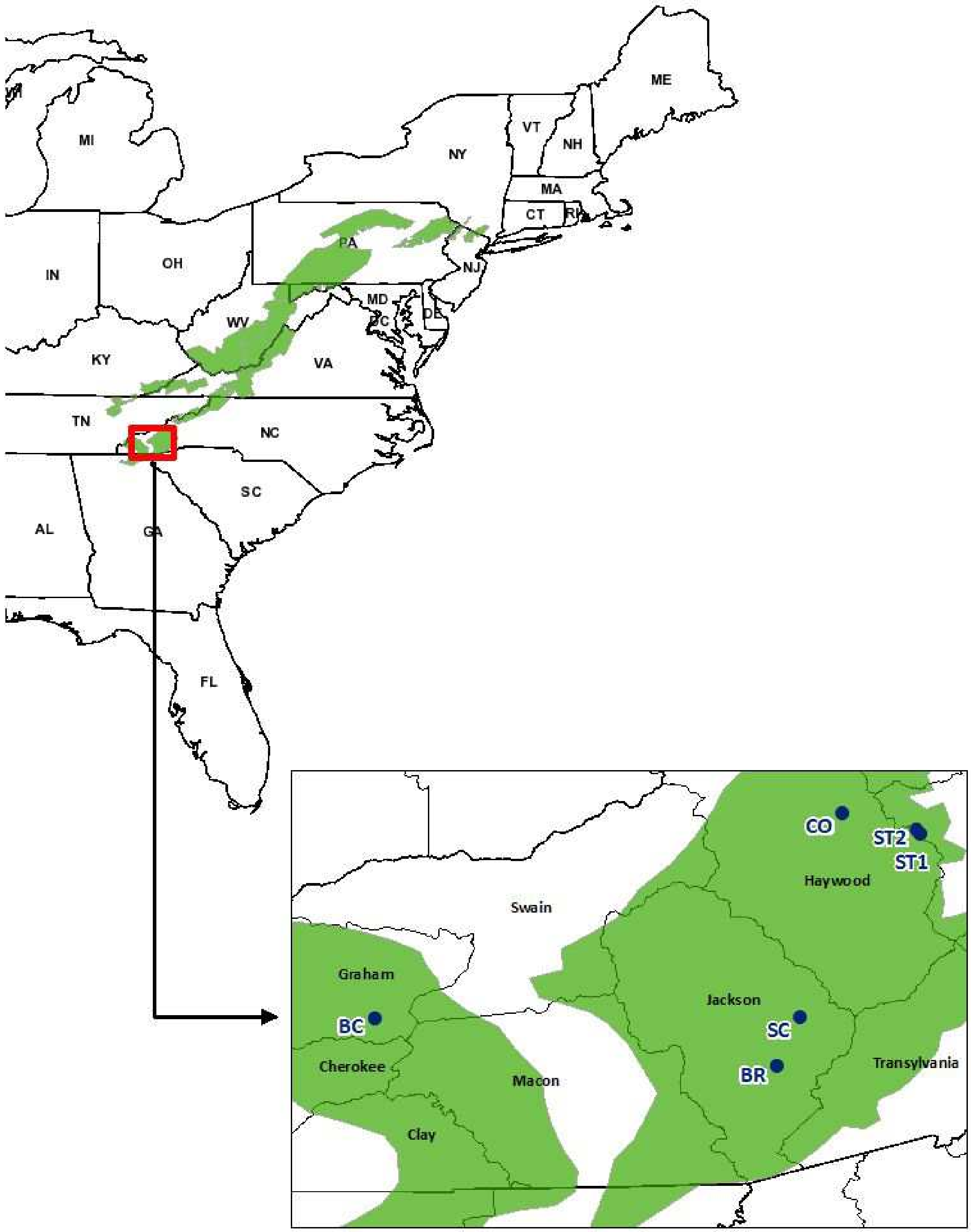

Fig. 1. Inset map of GWWA study sites. The green shaded regions represent GWWA Focal Areas in the Appalachian Mountains, designated by the GWWA Working Group. Sites included in this research project are represented on the inset map by blue circles labeled with site codes.

Two of the study sites were located on private land north of Canton (Haywood County) and are henceforth referred to as ST1 and ST2. The landowner is engaged in active management for wildlife, including GWWA, on the property. ST1 is characterized by upland field habitat with patchy shrubs and is surrounded by hardwood forest. A photograph taken at the ST1 site is shown in Fig. 2. This site is composed of habitat typical of that used by breeding GWWA. Two male GWWA established adjacent territories in this area; the two territories and males occupying those territories are referred to as ST1-A and ST1-B. The elevation at ST1-A is 1233 m and the elevation at ST1-B is 1250 m.

The ST2 territory is located approximately 0.8 km from the ST1 site and is at an elevation of 1266 m. The majority of the land area is forested and is dominated by oaks and other hardwood species. The area is traversed by several grassy/gravel roads.

Fig. 2. Photograph of ST1 study site, showing typical GWWA breeding habitat. This photograph was taken on June 20, 2014.

CO, a private site in Haywood County, is situated next to a highway and is predominately shrubby with hardwood and pine trees interspersed. The area surrounding the GWWA territory is forested. Elevation of the site is 962 m.

The final site located on private land, referred to as BR, is located northeast of Glenville (Jackson County). This site is characterized by shrubby habitat with scattered canopy trees and is surrounded by tracts of hardwood/conifer forest. Two male GWWA territories were established at the site; the two territories and occupying males are referred to as BR1 and BR2. The BR1 territory is at an elevation of 1185 m and the BR2 territory is at an elevation of 1182 m.

The two sites in Nantahala National Forest, referred to as BC and SC, are located in Graham and Jackson counties, respectively. BC is located southeast of Robbinsville at an elevation of 757 m. The site is within a power line right-of-way and is predominately shrubby habitat, bordered by hardwood/pine forest. The GWWA territory was delineated on one end by a small creek and, on the opposite side of the creek, by a tall, steep embankment. SC, located east of Tuckasegee in Jackson County, is at an elevation of 1404 m. One male GWWA established a territory at the site, which is characterized by a mix of old field habitat and hardwood forest.

Bird Surveys

In late April 2014, I began surveying potential study sites for returning GWWA. The point count (i.e., stationary count of all bird species seen and/or heard) protocol was adapted from a standardized protocol established by the GWWA Working Group (Roth et al. 2012). GWWA have two song types—the primary ("Type 1") song is used to attract females (Confer et al. 2011) and is often sung by paired males on their territories (Dunn and Garrett 1997). "Type 2" song is generally sung during intense intrasexual territorial conflicts (Confer et al. 2011). Each GWWA survey consisted of a 3-minute passive count, 5 minutes of playback of GWWA Type 1 song, 1 minute of silent observation, 1 minute of GWWA Type 2 song, 1 minute of silent observation, 5 minutes of "mobbing" playback (Eastern Screech-Owl [*Megascops asio*] calls and Carolina Chickadee [*Poecile carolinensis*] mobbing calls), and 1 minute of silent observation. All bird species seen or heard during the protocol were noted. Sites where GWWA were observed were later revisited to determine the number of male GWWA present. Surveys were completed by mid-May.

Point counts were conducted at 16 sites. A list of non-GWWA bird species seen or heard during these point counts is shown in Appendix A. A map displaying locations of surveys is shown in Appendix B. At five of the sites listed in Appendix A, a point count was conducted at a second location >200 m away from the first point to both ensure adequate survey coverage of the area and increase likelihood of detection of birds that may have been missed at the first survey location due to traffic noise, etc. Bird observations from pairs of point counts were combined under one site heading in Appendix A.

Territory Mapping

At sites chosen for the study, males were located and tracked beginning in early May. A total of eight male GWWA were included in the study. Territory mapping was conducted between 7:00 a.m. and 1:00 p.m. Locations of singing perches were marked in a Garmin Oregon 450 Global Positioning System (GPS) unit; the accuracy of the unit is <10 m. Additionally, behaviors such as foraging and territorial disputes were noted and locations marked. For cases in which a male GWWA was singing but the location was inaccessible due to steep terrain or dense vegetation, the distance from the observer to the bird was estimated and marked in the GPS unit. Observations of females were sporadic but were incorporated into territory maps. Territory mapping was completed in early July.

GPS waypoints were loaded into ArcMap (version 10.1, 2012, Esri) and the Minimum Bounding Geometry tool was used to demarcate a polygon representing each territory. Points and territory polygons were projected into North American Datum 1983 Universal Transverse Mercator Zone 17N for analysis.

Density of male GWWA at a site was determined by dividing the number of males on territory by the total area the territories encompassed. At sites where two males defended adjacent territories, the density was calculated as two divided by the total area encompassed by both territories.

Aggression Trials

Aggression trials were conducted from May 23 to June 18. Approval for the research was granted by the Western Carolina University Institutional Animal Care and Use Committee (approval number AUR 2014-001). Two or more trials were completed for each territory-holding male. Subsequent trials conducted on a given male were conducted at least six days apart. Protocol involved the use of playback to elicit a response from the male and followed that used by Scales et al. (2011). Conspecific song was played for 6 minutes from an mp3 player and portable speaker; playback was followed by 3 minutes of silent observation.

The sound files used in this study were generally composed of a combination of Type 1 and 2 songs. Two different sources for sound files were used. The first file was provided by Audubon North Carolina and included both song types; the location at which the bird was recorded is unknown. The second source for sound files was the Cornell Lab of Ornithology's Macaulay Library; files were recorded in New York (Type 1 song, #163386, MD Medler) and Maryland (Type 2 song, #107341, WL Hershberger). Sound files from the Macaulay Library were selected primarily based on quality; file duration was also taken into account so as to minimize the amount of looping required. Two aggression trial sound files, each composed of 3 minutes of Type 1 song followed by 3 minutes of Type 2 song, were generated using GoldWave software (version 5.70). Each file contained either Audubon North Carolina recordings or

Macaulay Library recordings—i.e., aggression trial files did not combine recordings from the two sources. Some background noise was removed from the files to increase sound quality.

The sound file used during the first trial for each male was randomly chosen; the alternate sound file was used for the second trial. Aggression trials for the ST1-B and ST2 males were the first trials conducted and utilized only Type 1 song from the Audubon North Carolina recording. After those trials were conducted, I decided to use both song types in all subsequent trials.

For each trial, the speaker was placed near the center of the male's territory, which was determined based on previous observations of his behavior. The speaker was placed 1-1.5 m high in a small tree or shrub. Flagging was placed on either side of the speaker at 2, 4, 8, and 16 m to facilitate determinations of distance. If the male was observed singing in the vicinity prior to the start of the trial, I waited until he had either stopped singing or moved out of the vicinity. Observations were made from a point >20 m from the speaker. Behaviors exhibited by the male, such as distance of approach to the speaker and number of songs sung in response, were recorded during playback and for 3 minutes following playback. The male's approximate distance from the speaker was recorded every 5 seconds during the trial. The average distance of approach to the playback speaker was calculated for each trial. Close approach to the speaker was interpreted as aggressive behavior (Hyman and Hughes 2006).

Vegetation Surveys

Vegetation surveys were completed between July 15 and August 12. I chose to conduct vegetation surveys after the prime nesting period had ended in order to reduce the likelihood of negatively affecting nest attempts because the surveys required prolonged presence of the researcher within study plots and necessitated some disturbance of vegetation while accessing the plots. Locations of vegetation survey plots were determined using the Create Random Points tool in ArcMap. Five points, located at least 10 m apart, were selected for each territory. Several of the randomly generated survey points had to be relocated in the field due to dense vegetation or steep terrain that limited access to the points. In those cases, the point was relocated to an area that was generally representative of the vegetation structure at the original point.

At each vegetation survey point, a GPS unit was used to mark plot center and record elevation from waist height. Two 10-m ropes were used as transects and laid out from north to south and from east to west; thus, each survey plot was circular with a 5-m radius. Percent canopy cover was measured from the center of each plot using a spherical densiometer, facing each cardinal direction; these values were averaged to produce one canopy cover value per plot.

The height and density of vegetation were recorded using a combination of Robel pole measurements and visual estimates. The Robel pole used for this project was a 2-m PVC pipe marked in 10-cm increments with colored duct tape, with 14-cm spikes affixed to the bottom of the pole to enable it to stand upright. The design of the pole was adapted from the design suggested by Toledo et al. (2008). Vegetation height and density measurements were taken at the center of each plot and at the north, south, east, and west ends of the transects. Values were then averaged for each plot. Measurements and estimates were taken from the north side of each point, approximately 4 m from the Robel pole and approximately 1 m from the ground.

Shrub height was determined by multiplying the number of the lowest Robel pole segment not covered with vegetation by 10 cm and adding 14 cm to account for the length of the spikes. This method of determining vegetation height likely resulted in slight overestimates. However, since topographic variation within and across survey plots may have resulted in underestimates at some survey points, average values were most likely representative of shrub heights within the plots.

Protocol for measuring shrub density was modified from that specified by Herrick et al. (2009) and Smith (2008). Shrub density was measured by noting the number of bands at least 25% covered, dividing that number by 20 (the total number of pole segments), and multiplying by 100 to obtain a percentage.

Percent cover of shrubs, herbaceous plants, bare earth, and rock were measured at the center of each plot and at the north, south, east, and west ends of the transects using a 1-m quadrat. Measurements were averaged to yield one value per plot for each variable. In areas where dense vegetation or steep terrain limited access to the ends of the transects, visual estimates were made. For the purposes of this study, non-woody plants were included in measurements of shrub cover if they contributed vertical structure within the sampled plots.

Samples were collected from dominant herbaceous and shrub species within plots. No samples were collected if there were no dominant species present (i.e., if the species composition was fairly heterogeneous). Plant samples were refrigerated and later pressed. Each sample was identified to genus by H. Meeler, a graduate student in the Western Carolina University Biology department. Most grass samples were unidentifiable to genus and thus were underrepresented in this analysis. Labeled samples were deposited into the university herbarium.

For each tree >10 cm dbh, its dbh was recorded. Dbh was measured using a dbh tape at 1.4 m above ground on the uphill side of the tree. If a tree trunk consisted of multiple stems, all stems were measured and the values added together to yield one value. The species or genus of each tree within the plot was recorded, if known. Some species were later identified by M. Hooker, a graduate student in the Western Carolina University Biology department, using photographs and leaf samples. To calculate basal area of sampled trees, the procedure developed by the Mississippi Department of Wildlife, Fisheries, and Parks (MDWFP) was followed. The basal area (BA) of each tree within a survey plot was calculated using the following formula: $BA = 0.005454 * dbh^2$. Dbh values were converted to inches for usage in this formula. The resulting BA values, with units of sq. ft, were converted to sq. m. BA values for all trees sampled within the five survey plots per territory were summed and divided by the total area of the plots to yield total BA per ha of survey plots.

LiDAR Data

LiDAR (Light Detection and Ranging) datasets for the study areas were downloaded from the US Geological Survey's CLICK (Center for LiDAR Information Coordination and Knowledge) website via the EarthExplorer database. Data were gathered in 2005 by the private company Fugro EarthData, formerly known as EarthData International. This was the most recent year for which free LiDAR data were available for the study sites. The map projection of the datasets used for this research was NAD 1983 North Carolina State Plane (Feet); thus, units used in LiDAR analysis differ from metric units used elsewhere in the research project.

The software program FUSION (version 3.42, 2014, R. McGaughey, Forest Service Pacific Northwest Research Station) was used to process and view LiDAR data. Protocol for use of the software was adapted from the FUSION online manual (RSAC). The LiDAR datasets were used to generate a reference image of the study sites. In ArcMap, a 100-m buffer was generated around each territory polygon; these shapefiles were used to clip the LiDAR datasets. Thus, for each territory, analysis of vegetation structure was conducted on data within the territory plus buffer area. The buffer size was set at 100 m to encompass forested edge near each territory.

Ground-level returns were filtered out from the LiDAR data and used to create a bare earth digital elevation model for each study site; this allowed for elevation values to be subtracted from the returns, thus generating a dataset composed only of above-ground returns (i.e., vegetation). Models of vegetation density were generated for returns between 2 and 5 ft above ground (i.e., shrubs) and for returns between 20 and 100 ft above ground (i.e., canopy trees). Shrub and canopy cover were selected for analysis because (1) those vegetation layers are consistently investigated in research on GWWA breeding habitat and were directly measured in the field for this study, and (2) the LiDAR returns for those layers are more easily extracted than, for example, an herbaceous or ground cover layer.

The resulting model for each territory was exported to ArcMap, where the Raster Calculator tool was used to determine the percent area with ≥ 50% density of shrub layer and canopy layer returns. Density of returns refers to the number of laser pulse returns striking objects within a certain height range divided by the total number of laser pulses. Thus, density of returns is analogous to the amount of shrub or canopy cover in a given area.

Data Analysis

Data analysis was conducted using R (version 3.1.2, 2014, The R Foundation for Statistical Computing) in combination with JGR (version 1.7-16, 2013, M. Helbig, S. Urbanek, and I. Fellows), Deducer (version 0.7-7, 2014, I. Fellows), and the ggplot2 package (version 1.0.1, 2015, H. Wickham and W. Chang). Regression analysis was performed on territory characteristics (e.g., territory size, canopy cover, and shrub density) versus trial 1 approach distance to test whether correlations existed between male aggression and measures of territory characteristics. A two-tailed paired t-test and regression analysis were conducted on trial 1 versus trial 2 approach distances to determine whether (1) intra-individual differences in aggression existed, or (2) there were correlations between aggressive responses given by each male. One-way ANOVA was performed to ascertain whether there were differences in vegetation characteristics between territories. Significant ANOVA results were further analyzed using post hoc Tukey HSD tests.

RESULTS

Bird Surveys

Of the 16 points at which surveys were conducted, six had GWWA present. I used four of these sites in the study and later added two other sites after staff from state and federal agencies conducted GWWA surveys in those areas and found GWWA on territory. At two of the sites, two males held adjacent territories (BR1/BR2 and ST1-A/ST1-B).

Incidental Observations

GWWA Nests

Two GWWA nests were observed during the field season—one nest each at the ST1-A and ST2 sites. Both nests were at or near ground level. The ST1-A nest was near the edge of a shrubby patch. The ST2 nest was placed at the edge of a mowed but generally unused roadbed (Fig. 3).

Direct observations of fledgling activity were made at the BR1 and ST1-B sites, where parents were observed bringing food to fledglings hidden in vegetation along the forested edges of the territories.

Fig. 3. GWWA nest and nest site on ST2 territory. The photo at right shows the grassy roadbed and edge at which the nest was placed; the nest location is circled. The landowner set up wildlife cameras after the nest was discovered. The nest was found on 5/29 and contained five eggs. It was rechecked on 6/5 and all eggs appeared to have hatched (photo at left). The nest was not checked after that date. A female GWWA was seen gathering food on 6/28 about 35 m from the nest but fledglings were not directly observed.

Observation of Hybrid Individual

On June 6, 2014, a male Brewster's Warbler was observed at the CO site, singing a typical Type 2 GWWA song less than 70 m from the GWWA territory (Fig. 4). It is unknown whether the bird remained in the area and attempted to breed, as it was not directly observed after that date.

Brewster's Warbler (BRWA) is the more common of two phenotypes resulting from hybridization between GWWA and the congener Blue-winged Warbler (BWWA). BRWA exhibits the dominant phenotypic characteristics of genetically pure GWWA and BWWA parents (Confer et al. 2011).

Fig. 4. Photographs of male Brewster's Warbler observed singing at CO site on June 6.

General Territory Characteristics

Sizes of individual territories determined through mapping, as well as density of males at each site, are shown in Table 1. Data on the two sites with adjoining territories (BR1+BR2 and ST1-A+ST1-B) are displayed at the bottom of the table. Total territory size of the "paired" territories was determined using a polygon that encompassed all territory mapping points for both males. Note that, for the BR and ST1 sites, the total territory size is less than the sum of the areas of the individual territories; thus, there was some overlap in the mapped territories when males occupied adjoining territories. The mean territory size was 1.82 ha (n=8, SD=1.32 ha) and the mean GWWA density was 1.02 ± 0.74 males/ha (mean ± SD).

Table 1. Sizes of male GWWA territories and density of males at each site. Data on the two sites with adjoining territories (BR1+BR2 and ST1-A+ST1-B) are displayed at the bottom of the table; total territory size of the “paired” territories was determined using a polygon that encompassed all territory mapping points for both males.

Territory	Territory size (ha)	Density (males/ha)
BC	1.30	0.77
BR1	1.98	--
BR2	2.70	--
CO	0.58	1.74
SC	4.26	0.23
ST1-A	0.33	--
ST1-B	0.87	--
ST2	2.54	0.39
BR1+BR2	3.71	0.54
ST1-A+ST1-B	1.01	1.98

Aggression Trials

There was no significant difference in approach distance between trial 1 (7.04 ± 2.42 m, mean ± SD) and trial 2 (7.54 ± 4.03 m, mean ± SD) (paired t-test: $t(5) = -0.55$, $p = 0.61$). Conversely, there was no correlation between approach distances for trial 1 and trial 2 ($R^2 = 0.25$, $F_{1,4} = 1.33$, $p = 0.31$).

The male occupying the CO territory responded to the first playback trial but there was no discernible response to a second playback trial conducted eight days later. There was a discernible response from the BR1 male during only one trial; another trial was conducted but it could not be confirmed whether the bird that responded was a GWWA, as it was observed only briefly, from afar and in dense vegetation, and did not vocalize or reappear. Thus, two males were removed from analysis of trial 1 versus trial 2. Only one male (SC) responded to a third aggression trial; however, the results of the trial were excluded from analysis because windy conditions during the trial likely affected his ability to hear playback and thus may have influenced the intensity of his response.

Vegetation Surveys

Genera of dominant shrub and herbaceous plant species found within sampled plots are shown in Table 2. Grass species are underrepresented because samples collected and brought back to the lab were generally not identifiable to genus. *Rubus* species were the most common plants found in sampled plots within four of the eight territories.

Table 2. Genera of dominant shrub and herbaceous plants found within vegetation survey plots. Genera are listed in alphabetical order.

Territory	Dominant plant genera
BC	*Clematis, Impatiens, Rubus*
BR1	*Rubus*
BR2	*Daucus, Dicanthelium, Rubus, Thelypteris, Vaccinium*
CO	*Solidago*
SC	*Fragaria, Rubus, Vicia*
ST1-A	*Aster*
ST1-B	*Ambrosia, Aster, Glechoma, Polygonum, Solanum*
ST2	*Actaea, Circaea, Clematis, Solidago*

Average values for dbh of trees sampled within vegetation plots, along with the total tree basal area, are shown in Table 3. Survey plots within the BC territory did not contain trees (Table 3). The two territories with the largest average dbh, BR2 and ST1-A, also exhibited the highest amount of variation with regard to dbh. The territory with the highest total basal area (ST2) contained the largest number of trees within sampled plots; this territory consisted of substantially more forested habitat than did the other territories.

Table 3. Average dbh (cm), SD of dbh, and basal area (m^2/ha) of sampled trees per territory. Total basal area was calculated by adding the basal area of all trees sampled within a territory and dividing by the total area of the five vegetation survey plots.

Territory	Average dbh (cm) of trees within sampled plots	SD of dbh (cm)	Total basal area (m^2/ha) of sampled trees
BC	N/A	N/A	N/A
BR1	25.0	19.8	9.4
BR2	39.5	33.1	13.8
CO	16.9	5.5	3.7
SC	17.8	8.5	9.2
ST1-A	39.3	25.3	16.2
ST1-B	30.9	24.4	23.7
ST2	27.3	21.8	30.7

Average values for all other characteristics measured within sample plots are shown in Table 4. Territories were situated at elevations spanning a range of more than 640 m (1155 ± 192 m, mean ± SD). Average percent canopy cover varied widely across territories (56.1 ± 34.6%, mean ± SD). Territories exhibited a wide range of shrub heights (143 ± 45.5 cm, mean ± SD) and slightly less variable shrub densities (58.5 ± 23.2%, mean ± SD).

Table 4. Average values of characteristics measured within vegetation survey plots.

Territory	Elevation (m)	Average % canopy cover	Average % shrub density	Average shrub height (cm)	Average % herb cover	Average % shrub cover	Average % bare earth cover	Average % rock cover
BC	758	19.2	78.2	177.6	19.2	62.4	10.0	8.4
BR1	1185	46.1	69.6	166.0	30.4	61.6	8.0	0.0
BR2	1182	45.4	43.0	110.0	53.2	22.0	24.8	0.0
CO	962	52.8	71.4	166.8	43.6	53.6	2.8	0.0
SC	1404	64.0	53.0	131.6	43.2	38.0	18.8	0.0
ST1-A	1233	52.5	48.6	124.8	74.8	24.4	0.8	0.0
ST1-B	1250	85.1	56.6	138.0	50.8	46.0	3.2	0.0
ST2	1266	84.0	47.8	124.8	72.8	20.0	7.2	0.0

There were significant differences between territories with respect to elevation, percent canopy cover, percent cover of herbaceous plants, percent cover of shrubs, and percent cover of bare earth (Table 5). There were no significant differences with respect to shrub density ($F_{7,32}$= 1.75, p = 0.13), shrub height ($F_{7,32}$= 1.60, p = 0.17), or percent cover of rock ($F_{7,32}$= 1.0, p = 0.45).

Table 5. Significant results of ANOVA comparing GWWA territory characteristics.

Source	Sum of squares	Df	Mean squares	*F*	*P*-value
Elevation					
Groups	1430536	7	204362	1689	< 0.0001
Error	3856	32	121		
Total	1434392	39			
Percent canopy cover					
Groups	16409	7	2344	2.47	0.04
Error	30322	32	948		
Total	46731	39			
Percent herb cover					
Groups	12739	7	1820	3.43	0.008
Error	16995	32	531		
Total	29734	39			
Percent shrub cover					
Groups	10763	7	1538	2.67	0.03
Error	18453	32	577		
Total	29216	39			
Percent bare earth cover					
Groups	2443	7	349	2.37	0.04
Error	4693	32	147		
Total	7136	39			

Tukey HSD tests showed that BC had significantly less canopy cover than both ST1-B (p = 0.04) and ST2 (p = 0.04). Additionally, BC had significantly less herbaceous plant cover than both ST1-A (p = 0.01) and ST2 (p = 0.02). All territories, with the exception of BR1/BR2, ST1-A/ST1-B, and ST1-B/ST2, differed significantly from each other with respect to elevation ($p < 0.01$). No significant differences between territories were found with respect to percent cover of shrubs or of bare earth when a Tukey HSD test was performed.

LiDAR Data

Results of LiDAR data analysis revealed more variability with respect to density of canopy returns than to density of shrub returns (Fig. 5). Across all territories, the percent area with $\geq 50\%$ density of canopy returns averaged 22.8 ± 14.0%, whereas the percent area with $\geq 50\%$ density of shrub returns averaged 20.1 ± 7.0%. The BC territory contained the largest percent area of high-density canopy and shrub returns.

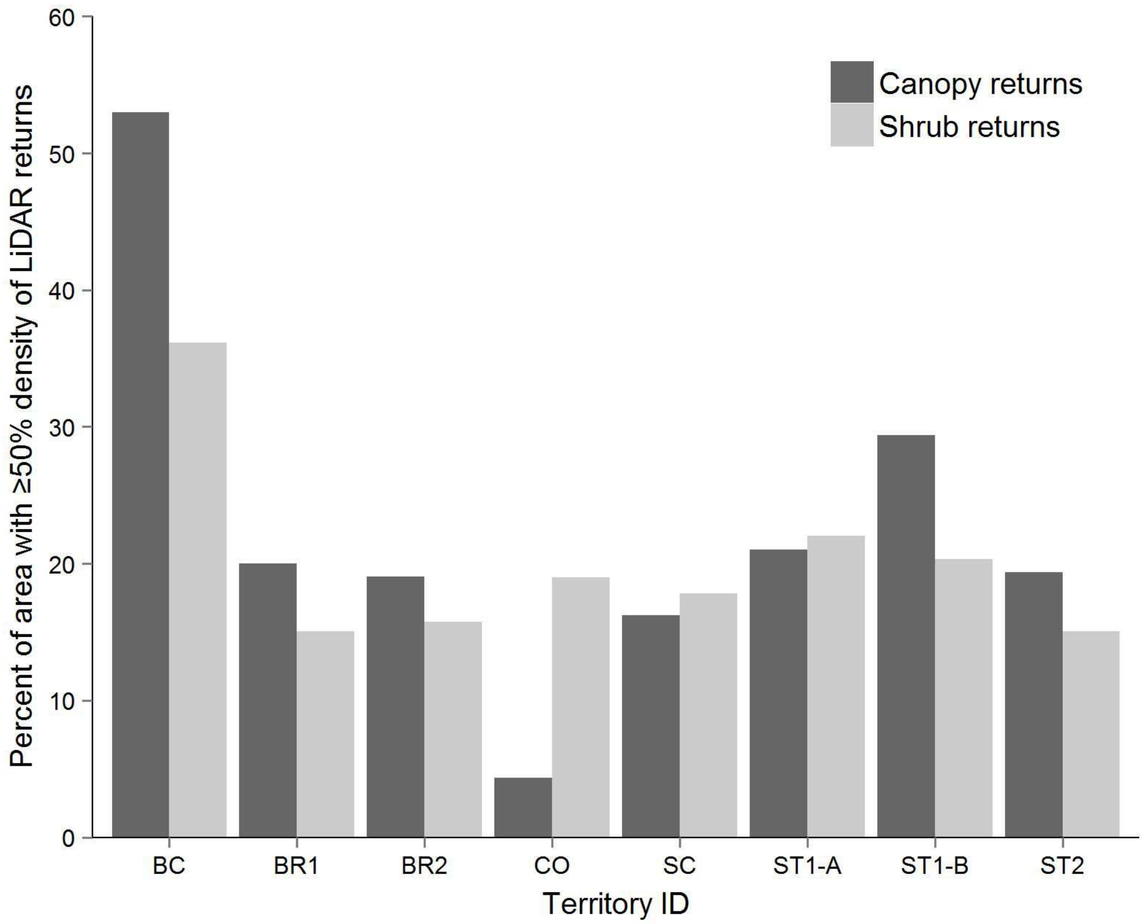

Fig. 5. Territory percent area containing ≥50% density of shrub and canopy layer LiDAR returns.

Correlations between Male Aggression and Territory Characteristics

There were significant correlations between male aggression and tree dbh, shrub density, and shrub height (Table 6). A negative relationship was found between tree dbh and distance of approach to the playback speaker ($b = -0.21$; Fig. 6). Shrub density and shrub height were positively correlated with approach distance ($b = 0.15$ and $b = 0.083$, respectively; Figs. 7 and 8). Amount of shrub cover was also positively correlated with approach distance but the result was not quite significant at the $p < 0.05$ level (Table 6).

Table 6. Results of linear regression analysis of male aggression versus territory characteristics. For all characteristics, with the exception of territory size, male density, total tree basal area, and LiDAR return densities, analysis was conducted on averages of measurements made in the field. Distance of approach to the playback speaker during trial 1 was used as the outcome variable. Asterisks denote significance at the $p < 0.05$ level. Analysis was conducted on 1 and 6 df, except for tree dbh and total basal area (df = 1,5).

Characteristic	R^2	F	P-value
Territory size	0.03	0.17	0.70
Male density	0.01	0.08	0.79
Elevation (m)	0.28	2.32	0.18
Tree dbh (cm)	0.62	8.22	0.04*
Total basal area (m^2/ha)	0.05	0.23	0.65
Canopy cover percent	0.05	0.31	0.60
Shrub density percent	0.65	10.93	0.02*
Shrub height (cm)	0.70	14.04	0.01*
Percent herb cover	0.23	1.80	0.23
Percent shrub cover	0.44	4.71	0.07
Percent bare earth cover	0.19	1.42	0.28
Percent rock cover	0.16	1.12	0.33
LiDAR shrub density	0.08	0.55	0.49
LiDAR canopy density	0.01	0.06	0.81

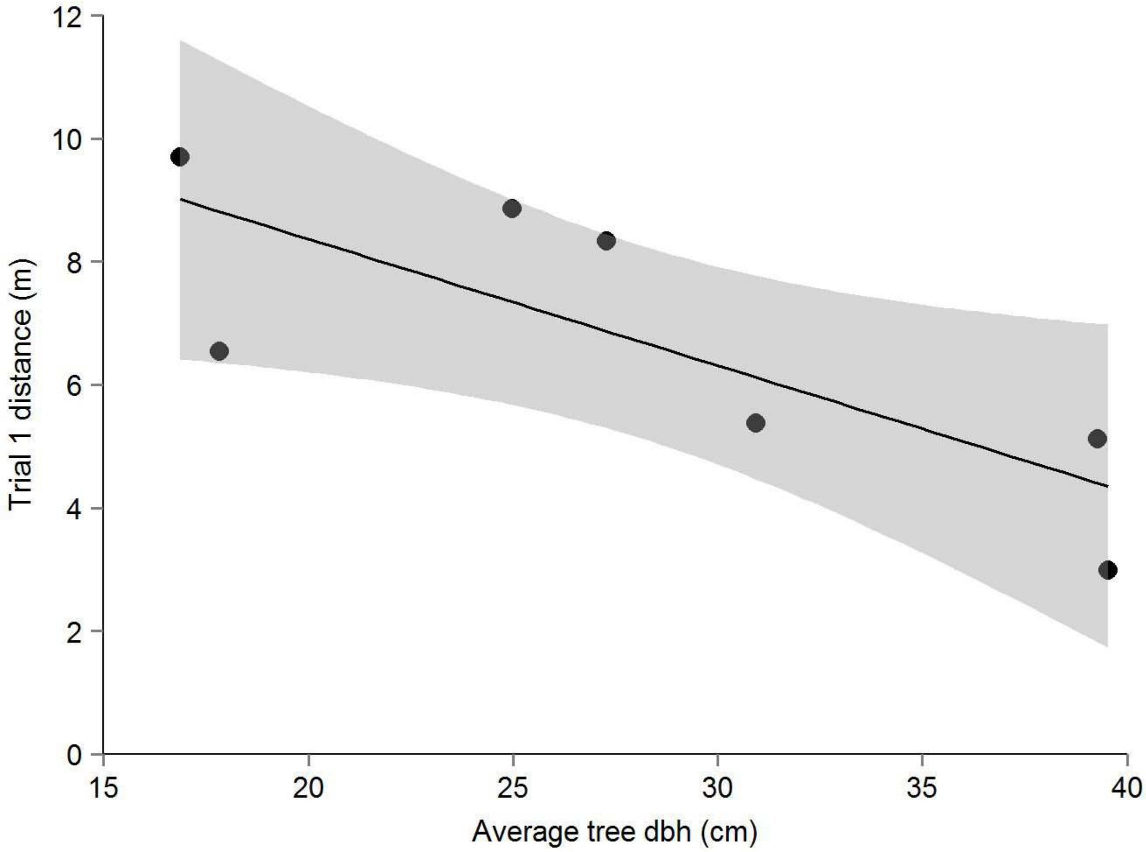

Fig. 6. Average tree dbh versus trial 1 distance of approach to playback speaker. Equation of the regression line is y = 12.5 - 0.21x (R^2 = 0.62, $F_{1,5}$ = 8.22, and p = 0 .04). The 95% confidence band is shown. Note that one territory (BC) was excluded from this analysis because no trees were found within sampled plots.

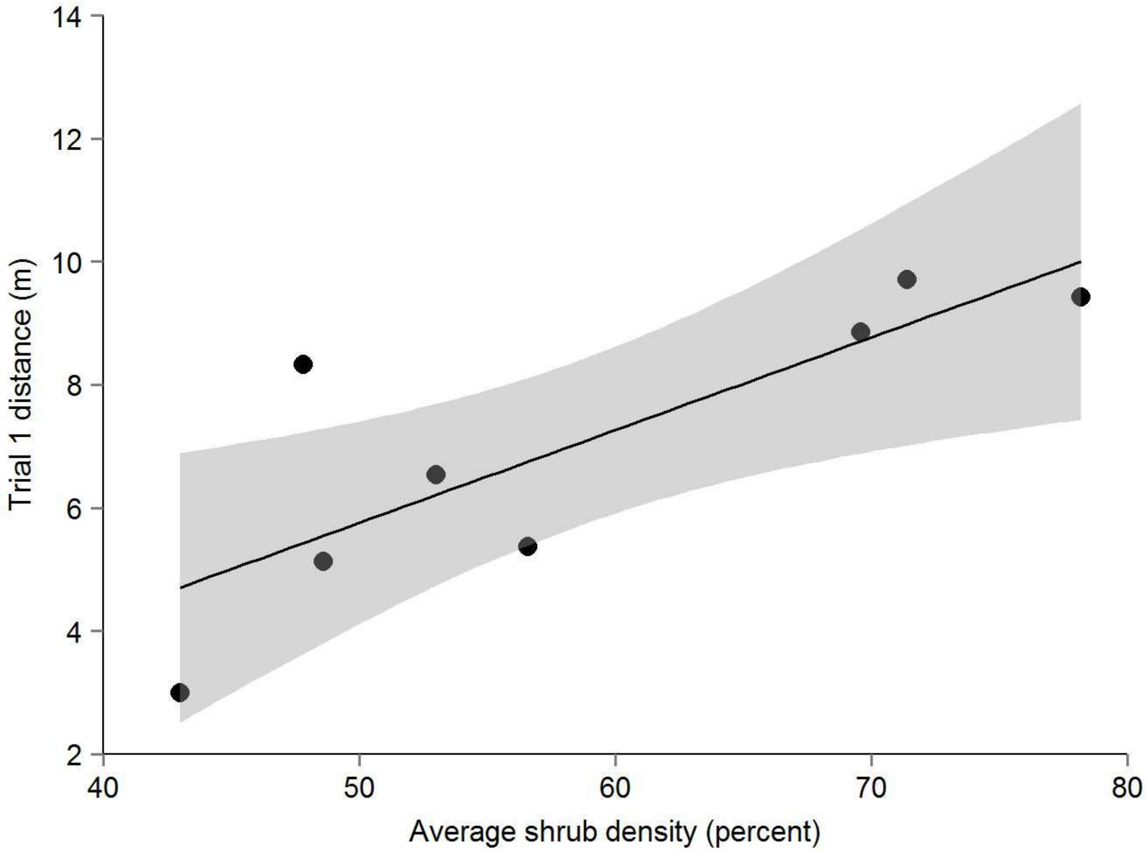

Fig. 7. Average shrub density percent versus trial 1 distance of approach to playback speaker. Equation of the regression line is y=-1.77+0.15x (R^2=0.65, $F_{1,6}$=10.93, and p=0 .02). The 95% confidence band is shown.

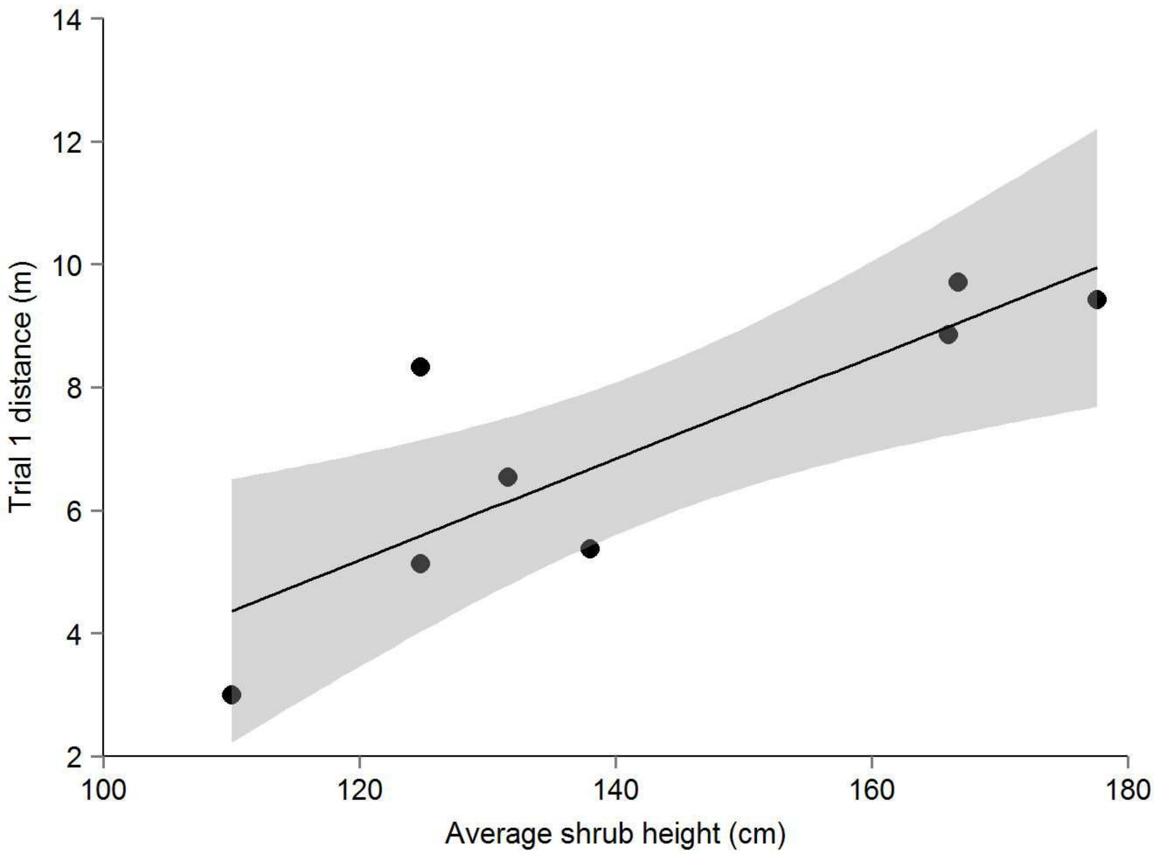

Fig. 8. Average shrub height versus trial 1 distance of approach to playback speaker. Equation of the regression line is $y = -4.72 + 0.083x$ ($R^2 = 0.70$, $F_{1,6} = 14.04$, and $p = 0.01$). The 95% confidence band is shown.

DISCUSSION

Incidental Observations: GWWA Nests and Brown-headed Cowbirds

A GWWA mated pair constructs a nest on or near the ground, often located along a microhabitat edge and supported by an herbaceous or woody plant stem (Confer et al. 2011). Thus, locations of the two nests found during this study were comparable to those documented by other researchers. Both nests were located on or near a shrubby microhabitat edge.

GWWA nests are sometimes parasitized by Brown-headed Cowbirds (Confer et al. 2011), which lay their eggs in host birds' nests and leave the host parents to provide parental care for the cowbird chicks. Brown-headed Cowbirds were not observed at the sites used for this project; the species was not detected during preliminary point counts (see Appendix A) or during subsequent site visits.

Territory Size and Male Density

The mean GWWA territory size determined in this study (1.82 ± 1.32 ha; mean ± SD) was slightly larger than mean territory sizes found in other studies in which similar territory mapping protocols were used (e.g., Aldinger et al., 2014; Patton et al., 2010). However, the SD of the mean territory size found in my study was also larger than calculations of SD/SE in those studies; thus, when the SD is taken into account, the mean territory size is comparable to that found by other researchers. Aldinger et al. (2014) found that 90% of *Vermivora* (i.e., GWWA, BWWA, and hybrid) territories were <3 ha in size. Results of my study demonstrate that approximately 88% of mapped territories were <3 ha. This distribution of territory sizes is likely related to a combination of factors, such as amount of area needed to support GWWA adults and fledglings and sizes of available habitat patches exhibiting sought-after vegetation characteristics.

Roth and Lutz (2004) mapped male GWWA territories in Wisconsin and found that the mean density of territorial males ranged from 0.01 to 0.55 males/ha, depending on the dominant size class of aspens growing within the territories. Results of territory mapping conducted by Aldinger et al. (2014) showed that densities ranged from 1.05 to 3.37 males/10 ha (or 0.105 to 0.337 males/ha) across sites with differing management techniques. Kubel and Yahner (2008) found that male density at sites in Pennsylvania varied from 0.47 to 0.79 males/ha. Thus, the highest densities determined in this study (Table 1) are considerably higher than those found by other researchers. One possible explanation for this difference is the distribution of males across a site and the researchers' method of determining density. For example, Aldinger et al. (2014) studied male GWWA whose territories were distributed across large areas; their calculations of density incorporated land area that was not part of males' mapped territories (K. Aldinger, personal communication). In my study, there did not appear to be unclaimed space between neighboring territories (i.e., neighboring males held territories directly adjacent to each other), which may explain why calculated densities are higher than those found in other studies.

Male Aggression

Male GWWA showed varied responses to playback during the first aggression trial. As far as I know, there are no published studies on male GWWA aggression and, thus, I am unable to compare my results to those of other researchers. Researchers studying GWWA in northwestern NC and eastern TN investigated relationships between male plumage characteristics and aggression; however, the results of the study have not yet been published (A.

Tisdale, personal communication). Territoriality and singing by male GWWA are related to the birds' breeding cycle, with males remaining territorial until nesting begins (A. Tisdale, personal communication) and resuming singing and other territorial behaviors after the onset of incubation (Confer et al. 2011). Patterns of male aggression that may indicate timing of egg-laying and incubation are difficult to discern from the results of this study, as data on nesting were not systematically gathered.

Differences in approach distance during aggression trials may be related to personality differences—i.e., aggressive responses that are consistent over birds' lifetimes. Nowicki et al. (2002) found that responses of male Song Sparrows to territory intrusion in the form of conspecific song playback were consistent within a breeding season, with more aggressive males consistently approaching the playback speaker more closely than less aggressive males. In combination with personality-driven responses are the effects of factors such as age and experience. Hyman et al. (2004) demonstrated that male Song Sparrows that had held territories at a site in previous breeding seasons were more aggressive than males new to the site and proposed that some variation in aggressive response may be due to age of the birds.

There was no correlation or significant difference between approach distances during trials 1 and 2. It is unknown whether the nonsignificant correlation between trial measurements is a reflection of intra-individual variability of aggressive response and/or a result of uncertainty related to individual male identification. Due to a lack of sufficient time and resources to color-band GWWA, male identities were determined by observations of singing locations and by distinctiveness of songs. It is possible that males were misidentified during follow-up aggression trials, especially at sites where two males held adjacent territories. Territory mapping by Aldinger et al. (2014) demonstrated some tendency of males to shift their territories and for unmated males to wander in search of females; these behaviors may have been exhibited by males included in this study and, thus, may have influenced results of follow-up aggression trials.

It is interesting to note that the male with the closest approach distance (BR2) was the only male in this study that alternated between the Blue-winged Warbler and Golden-winged Warbler Type 1 songs. Based on observation of plumage characteristics, he did not appear to be a hybrid. According to Dunn and Garrett (1997), observations have been made of GWWA that appeared to be phenotypically pure yet sang the Blue-winged Warbler song. The mechanisms of this discrepancy are unknown, although it seems likely that these males spent considerable amounts of time during their first year in areas dominated by singing male Blue-winged Warblers. Research conducted on other oscine species has shown that juveniles learn songs from neighboring conspecifics (Sibley 2001). The similarity between both Type 1 and Type 2 songs of Golden-winged and Blue-winged Warblers may complicate song learning by juveniles living in areas occupied by both species and, thus, may influence the likelihood that those males will later sing songs of the congener species.

Vegetation Characteristics—Measured in the Field

The dominant plant species found within vegetation sample plots are fairly typical of early successional habitats. Other studies (e.g., Aldinger et al., 2014; Patton et al., 2010) that present information on dominant plant species within GWWA territories have reported findings similar to those of my study. *Rubus* species were the most common plants encountered, dominating vegetation survey plots within four of the eight territories. The presence of *Rubus* spp. within GWWA territories may be an indication of habitat quality, as Aldinger et al. (2014)

found a positive association between GWWA nest survival rate and the amount of *Rubus* cover within a territory.

There was quite a bit of variation in total basal area (BA) between territories (Table 3). Vegetation survey plots within the BC site contained no trees, whereas plots at the ST2 site contained a total of 13 trees. The median and maximum BA in this study were 11.56 m^2/ha and 30.72 m^2/ha, respectively. Klaus and Buehler (2001) studied GWWA in Cherokee and Nantahala National Forests and found that basal area differed significantly between sites occupied by nesting GWWA and sites unoccupied by GWWA. Within occupied sites, basal area ranged from 0 to 35 m^2/ha, with a median of 10 m^2/ha, while basal area in sites not occupied by GWWA ranged from 0 to 48 m^2/ha, with a median of 40 m^2/ha. Thus, the total basal area of trees sampled in my study was comparable to that determined by Klaus and Buehler (2001).

Measurements of percent canopy cover were generally comparable to results of other studies. The average percent canopy cover for all territories included in this study was 56.1% (Table 4). Klaus and Buehler (2001) found that the median percent canopy cover ranged from 38.8% at nest sites to 63.8% at song perch sites—i.e., not located near a nest. Percent canopy cover determined by Patton et al. (2010), working on coal mine reclamation sites in Kentucky, ranged from 9.9 to 83.3%, with a mean of 44.8%. Aldinger and Wood (2014), studying GWWA in West Virginia, found that the average percent canopy cover in sampled plots within GWWA territories was 12.2%. Thus, the results of this study fall within the ranges of canopy cover percentages measured by Klaus and Buehler (2001) and Patton et al. (2010) but differ from results found by Aldinger and Wood (2014). The disparity between average percent canopy cover measured in this study versus that measured in the Aldinger and Wood (2014) study may be explained by the fact that those researchers worked in pasturelands; those habitats likely contain substantially less canopy cover than most of the GWWA territories included in my study, simply because of the difference in successional stage of the habitats. This variation across GWWA breeding habitats indicates that GWWA habitat preferences are not tightly constrained by the amount of canopy cover present. These patterns are consistent with the fact that GWWA nest on the ground (Confer et al. 2011) rather than in the canopy, and, thus, do not choose breeding territories based on the availability of suitable trees in which to nest.

Results for shrub height (Table 4) were similar to findings of other studies. The average shrub height for all territories was 142.5 cm, with a maximum of 177.6 cm. Patton et al. (2010) measured an average shrub height of 1.1 m and a maximum of 1.8 m. Contrasting with these results are those of Aldinger and Wood (2014), who found that average shrub height varied from 159.1 cm within 1 m of GWWA nests to 3.1 m within sampled plots at random locations within territories. As noted previously, differences in results may be related to the type of habitat in which each study was conducted; pasturelands studied by Aldinger and Wood (2014) have lower canopy tree density than sites included in my study and, thus, are likely to contain higher densities of tall shrubs.

ANOVA and subsequent Tukey HSD tests demonstrated significant differences between territories with respect to elevation, percent canopy cover, and percent herbaceous cover (Table 5). With the exception of three territory pairs (BR1/BR2, ST1-A/ST1-B, and ST1-B/ST2), all territories differed significantly with respect to elevation, indicating that GWWA breed at myriad elevations within the southern Appalachians. Canopy cover and herbaceous plant cover differed significantly between only a few territories. These results seem to suggest that canopy cover and herbaceous plant cover within individual territories tend to exhibit heterogeneity, perhaps due to the generally heterogeneous nature of early successional habitats.

Vegetation Characteristics—Comparison with LiDAR Results

Methodology for analysis of LiDAR data precluded the ability to conduct statistical analysis to determine whether significant differences existed between the territories, as each territory was represented by only one value for shrub and canopy layer returns (Fig. 5). However, values for percent area of dense shrub and canopy LiDAR returns can be qualitatively compared to measurements obtained in the field (Table 4). Results of LiDAR analysis correspond to data gathered in the field with respect to the range of values for percent canopy cover and percent shrub density. Percent canopy cover showed a wider range of values than did percent shrub density. This seems to indicate that, at least in the case of the males included in this study, shrub characteristics may be more important than canopy cover as a determining factor in breeding habitat suitability; in other words, choice of breeding habitat appears to be more constrained by amount and density of shrub cover than by amount of canopy cover. This is likely related to a combination of factors, such as GWWA nesting habits and predation pressures.

Some of the results for vegetation characteristics measured within sample plots are consistent with findings from LiDAR analysis. The BC territory had the highest average shrub height and percent shrub density (Table 4), as measured in sample plots. According to LiDAR analysis, this territory had the highest percent area with ≥ 50% density of shrub layer returns (Fig. 5). Thus, despite the fact that LiDAR data utilized in this study were acquired in 2005 and vegetation measurements were taken in 2014, the results of both analysis methods were concordant for this territory. One possible explanation for this is the fact that the BC territory is located within a power line right-of-way, which likely undergoes periodic management to facilitate access by utility workers; the area has therefore not experienced natural succession.

Other territories show somewhat consistent results when LiDAR data and in-the-field measurements are compared. Results of LiDAR analysis roughly correspond to direct measurements with respect to canopy cover for the BR1, BR2, ST1-B, and ST2 territories (Table 4, Fig. 5). Both analysis methods show the BR territories near the low end and the ST1-B and ST2 territories at the high end in terms of density of canopy trees. With respect to density of shrubs, LiDAR and direct measurements are congruent for BR2, SC, and ST2, with those territories containing lower shrub densities. The CO and ST1-B territories contain higher shrub densities according to both analysis methods.

While many of the territories show consistencies between the two analysis methods, some territories do not show consistent results. For example, the BR1 territory had high percent shrub density as measured in 2014 (Table 4), yet LiDAR results place that territory at the low end of percent area with high density of shrubs (Fig. 5). It is likely that the vegetation within the territory has increased in both density and coverage since LiDAR data were gathered in 2005. The territory is located on private property and, while the exact history of human activity at the site is unknown, vegetation management has likely changed over the years, possibly related to timing of land sales and clearing of land for access roads.

LiDAR canopy analysis results for the BC territory are inconsistent with measurements made in the field. BC was found to have the lowest average percent canopy cover as measured in the field (Table 4) but LiDAR analysis shows that it has the highest percent area with ≥ 50% density of canopy returns (Fig. 5). This may be explained by cutting of trees in the power line right-of-way (ROW) since LiDAR data were obtained in 2005. However, it is more likely explained by the contrast between direct measurements taken in the field and the method of LiDAR analysis. While vegetation was directly sampled only in plots within the GWWA territory (i.e., within the ROW), LiDAR analysis included a 100-m buffer around the territory. Since BC is located in a narrow power line ROW within forest, LiDAR results were likely skewed toward more densely forested habitat.

Comparisons between LiDAR data and direct measurements are somewhat ambiguous for several of the territories. With respect to density of canopy trees, the CO, SC, and ST1-A territories do not show consistent results (Table 4, Fig. 5). LiDAR data show that the CO and SC territories have lower canopy tree density than was measured in the field, while ST1-A appears to have higher canopy tree density according to LiDAR analysis. Inconsistent results for CO and SC may be explained by the occurrence of succession and canopy tree growth since LiDAR data were obtained in 2005. Conversely, habitat management on the privately owned ST1-A site may explain why measurements obtained in 2014 demonstrate lower canopy tree density than do LiDAR data. Similarly, direct measurements show ST1-A has a relatively low shrub density, while LiDAR results demonstrate higher density. As mentioned previously with respect to canopy cover, this inconsistency may be due to active vegetation management by the landowner.

General consistencies between results of direct measurements and LiDAR analysis demonstrate that LiDAR can prove to be useful for investigations of landscape-level habitat characteristics. Due to the utility of and ease of access to remote sensing data, avian ecology researchers should consider utilizing LiDAR analysis to facilitate measurements of vegetation characteristics on a landscape scale.

Correlations between Male Aggression and Territory Characteristics

No clear relationship was found between GWWA density and males' approach distances to the playback speaker (Table 6). It was hypothesized that males in more densely-populated areas would display more aggression in response to playback of conspecific song. Yoon et al. (2012) found a positive correlation between population density and aggression of male Orange-crowned Warblers. The researchers used a combination of several different measures of aggression and corrected for breeding cycle stage. Differences in aggression trial methodology may explain why the results of this study contrast with results found by Yoon et al. (2012). However, at most sites included in my study, only one male GWWA was on territory; thus, investigations involving male density are not necessarily meaningful. Further research, especially in areas where multiple male GWWA defend neighboring territories, is needed to elucidate possible correlations between male GWWA aggression and population density.

Significant correlations were found between male aggressive response and tree dbh, shrub density, and shrub height (Table 6). Shrub density and shrub height were positively correlated with approach distance (Figs. 7 and 8, respectively), while tree dbh was negatively correlated with approach distance (Fig. 6). Note that approach distance and male aggressive response are negatively correlated—i.e., a smaller approach distance translates to a more aggressive response. A significant negative correlation between average tree dbh and approach distance indicates that more aggressive males occupied territories containing larger diameter trees. It is expected that, for most tree species, there is a positive relationship between dbh and tree height. Thus, tree dbh likely serves as a proxy for tree height, indicating that territories belonging to the most aggressive males contained larger, taller trees than did territories defended by less aggressive males. This is likely explained by the fact that, as mentioned previously, male GWWA utilize canopy trees as perches from which to sing for the purposes of mate attraction and territory defense. Taller trees facilitate wider broadcasting of song.

Shrub density was positively correlated with approach distance (Fig. 7), demonstrating that the most aggressive males defended territories consisting of less dense shrubs. The reasons for this relationship are unclear, as one would expect the most aggressive males to defend territories with higher densities of shrubs if higher shrub density impedes movement of terrestrial predators and, thus, contributes to greater GWWA nest success. However, it is possible that the less densely shrubby territories defended by the most aggressive males contained enough patches of shrubs to provide nesting areas protected from predators. There likely is a tradeoff between shrub density and presence of sufficient numbers of canopy trees within a given area due to sunlight availability. Thus, shrub densities within the range of 40-60% (Fig. 7) may represent the optimum density that limits predation pressures in areas with a sufficient number of canopy trees present.

In addition to the positive correlation found with respect to shrub density, shrub height was positively correlated with approach distance (Fig. 8). These results show that more aggressive males occupied territories with a shorter shrub layer. As in the case of shrub density, this may be related to the tradeoff between the growth of shrubs and the growth of canopy trees in a particular area. Male GWWA likely seek out habitats with some canopy trees and the presence of those trees may limit sunlight availability, thus inhibiting growth of tall shrubs. However, it is noteworthy that no significant relationship was found between percent canopy cover and either shrub density or shrub height.

As no trees were found in sampled plots within the BC territory, it was excluded from regression analysis of tree dbh versus approach distance. Thus, discussion of a correlation between the BC male's aggressive response and canopy cover is, by necessity, less robust than it would be if backed by statistical tests. BC had significantly less canopy cover than ST1-B and

ST2 (Tables 4 and 5). Compared to ST1-B and ST2, the male occupying the BC territory had a higher distance of approach to the playback speaker during the first aggression trial, indicating that his response to playback was somewhat less aggressive than responses of the other two males. Given that studies have shown a propensity for GWWA to defend territories containing at least a few canopy trees (e.g., Klaus and Buehler, 2001; Rossell, 2001) and Roth et al. (2014) found that GWWA nesting success at sites which retained some overstory trees was higher than at sites which had been clearcut, perhaps the absence of canopy trees within the power line ROW indicated that BC was of somewhat lower quality than the other GWWA territories. It is unknown, however, whether the presence of canopy trees along the boundary of the ROW was sufficient to meet criteria of habitat quality for GWWA.

Prior research on other avian species has revealed patterns in aggressive behavior and habitat quality. Research on Song Sparrows has shown correlations between male aggression and clutch size, indicating that more aggressive males defended higher quality territories (Scales et al. 2013); however, the researchers note that the exact causal relationship between male aggression and territory quality is unclear. Duckworth (2006) demonstrated a positive correlation between aggression of male Western Bluebirds and quality of the territories they successfully defended. Correlations found between male GWWA aggression and habitat characteristics seem to suggest that more aggressive males seek out particular vegetation attributes, such as larger trees and less dense shrub cover. Additional research is needed to more fully elucidate these patterns.

Follow-up with Landowners

Landowners and/or their liaisons were notified if GWWA were found on their property. Owners of the land on which the ST territories were located have historically conducted some habitat management for wildlife and have expressed interest in maintaining habitat for GWWA. Similarly, the BR landowners and their liaison wish to manage a portion of the site to maintain early successional habitat for GWWA and other species; trees—especially locust (*Robinia*)—are beginning to fill in at the site and the area may soon be unattractive to GWWA without management actions. At the CO site, staff members from the Natural Resources Conservation Service are involved in communicating management needs to the landowners.

Communication has been maintained with landowners on whose property GWWA were not found but that may, in the future, serve as appropriate habitat. For example, the RA and RE properties (see Appendices A and B), are located in areas where GWWA are likely to breed if there is sufficient habitat available. The landowners at both sites either have already engaged in habitat management for GWWA or are potentially interested in doing so.

Conclusion

Although the sample size for this study was small, the results provide a qualitative assessment of habitat characteristics within and surrounding GWWA territories, as well as of behavioral attributes of male GWWA. Measured territory characteristics, such as territory size and vegetation attributes, were generally consistent with results of published studies. LiDAR analysis served as an interesting method of determining habitat characteristics and, with some notable exceptions, was generally consistent with in-the-field measurements. Significant correlations were found between male aggression and tree dbh, shrub density, and shrub height, with tree dbh positively predicting male aggressive response and shrub density and height negatively correlated with male aggressive response.

Additional research is needed to determine whether aggression of individual male GWWA remains fairly consistent over the birds' lifetimes (i.e., whether aggression is a personality trait) and whether correlations exist between GWWA population density in a particular area and aggression of males defending territories in that area. Also, further research, such as studies incorporating analysis of nesting success, would clarify whether there are correlations between male aggression and quality of the habitats in which those males hold territories. Studies on other avian species have found positive correlations between aggression and both body size and reproductive output. If those correlations apply to GWWA, it is predicted that more aggressive males occupying higher quality territories would have higher reproductive success. Additionally, more aggressive males likely would be more successful than their less aggressive counterparts during competitive interactions with co-occurring species. Thus, detection of relationships between male GWWA aggression and measures of habitat characteristics has implications for conservation of the species.

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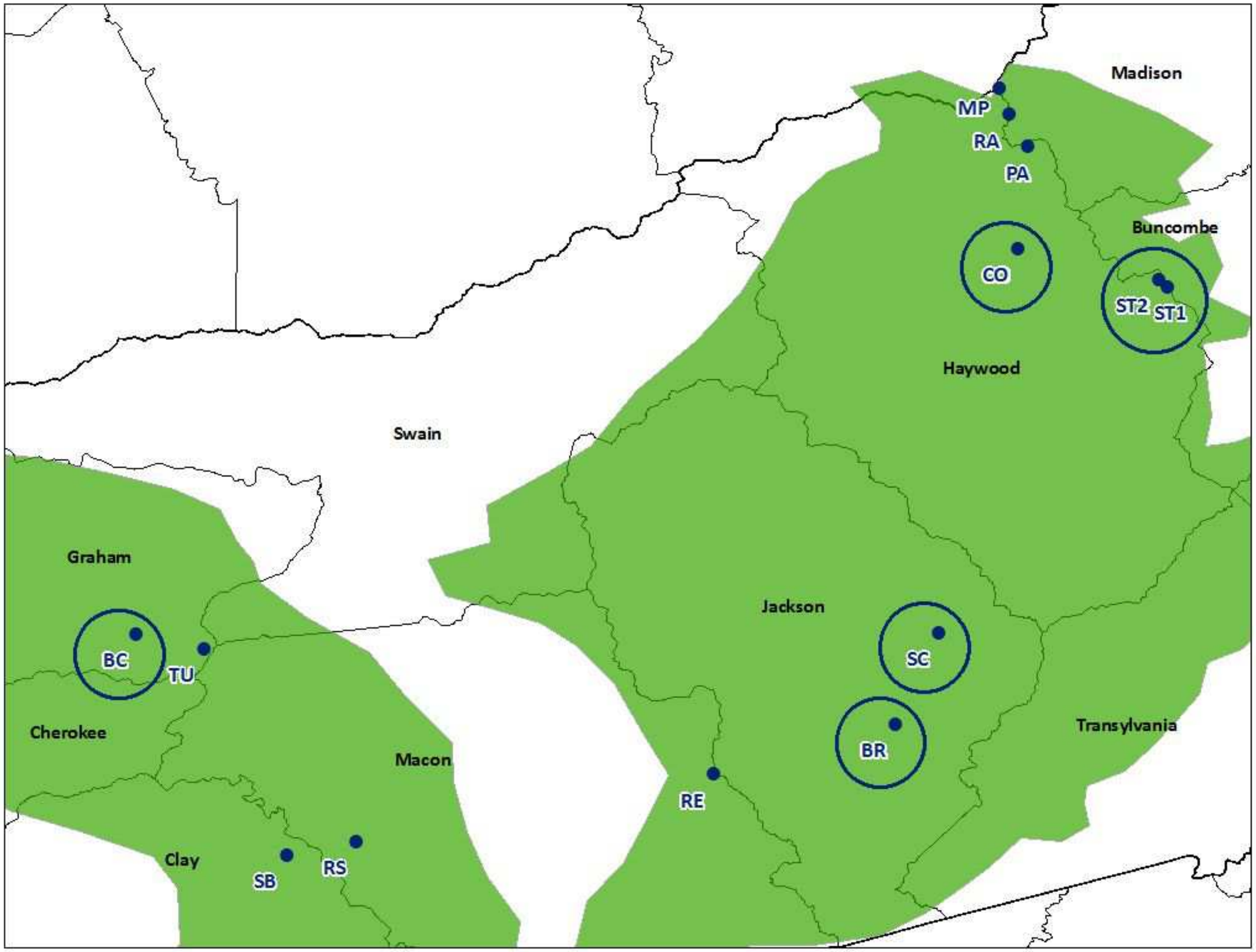
APPENDICES

Appendix A. Bird species detected during point counts. Locations of survey points are shown in Appendix B. Surveys were conducted on the following dates: BR: 5/12/14; SC: 4/26/14, 5/8/14; ST1: 4/28/14; ST2: 4/28/14; MP: 5/5/14; PA: 5/5/14, 5/17/14; RA: 5/5/14; RE: 5/9/14; RS: 5/14/14; SB: 5/13/14; TU: 5/2/14.

Common name	Scientific name	BR	SC	ST1	ST2	MP	PA	RA	RE	RS	SB	TU
Wild Turkey	*Meleagris gallopavo*				x							
Chimney Swift	*Chaetura pelagica*		x				x					
Ruby-throated Hummingbird	*Archilochus colubris*		x			x						
Red-bellied Woodpecker	*Melanerpes carolinus*		x									x
Yellow-bellied Sapsucker	*Sphyrapicus varius*		x									
Northern Flicker	*Colaptes auratus*		x			x	x	x		x	x	
Pileated Woodpecker	*Dryocopus pileatus*									x		
Acadian Flycatcher	*Empidonax virescens*										x	
Least Flycatcher	*Empidonax minimus*						x	x		x	x	
Eastern Phoebe	*Sayornis phoebe*			x	x							
Blue-headed Vireo	*Vireo solitarius*	x	x									
Red-eyed Vireo	*Vireo olivaceus*		x	x		x	x		x			x
Blue Jay	*Cyanocitta cristata*		x	x		x						x
American Crow	*Corvus brachyrhynchos*					x		x	x	x	x	
Common Raven	*Corvus corax*					x						
Carolina Chickadee	*Poecile carolinensis*	x			x		x			x		
Tufted Titmouse	*Baeolophus bicolor*		x	x						x	x	x
Red-breasted Nuthatch	*Sitta canadensis*					x						
White-breasted Nuthatch	*Sitta carolinensis*		x		x				x			x
House Wren	*Troglodytes aedon*									x		
Carolina Wren	*Thryothorus ludovicianus*		x		x					x	x	
Veery	*Catharus fuscescens*		x									
Wood Thrush	*Hylocichla mustelina*			x	x					x		
American Robin	*Turdus migratorius*		x		x	x			x	x		
Gray Catbird	*Dumetella carolinensis*		x		x	x	x	x		x	x	

Brown Thrasher	*Toxostoma rufum*		x			x				x		
European Starling	*Sturnus vulgaris*							x				
Cedar Waxwing	*Bombycilla cedrorum*					x						
Ovenbird	*Seiurus aurocapilla*	x	x	x		x	x	x	x	x		
Worm-eating Warbler	*Helmitheros vermivorum*								x			
Black-and-white Warbler	*Mniotilta varia*	x	x	x		x	x			x		
Common Yellowthroat	*Geothlypis trichas*		x			x	x					
Hooded Warbler	*Setophaga citrina*	x	x		x	x	x				x	x
American Redstart	*Setophaga ruticilla*	x					x				x	
Northern Parula	*Setophaga americana*	x								x		x
Blackburnian Warbler	*Setophaga fusca*	x										
Yellow Warbler	*Setophaga petechia*									x		
Chestnut-sided Warbler	*Setophaga pensylvanica*	x	x	x	x	x	x	x	x	x	x	
Black-throated Blue Warbler	*Setophaga caerulescens*		x			x				x	x	
Black-throated Green Warbler	*Setophaga virens*							x				
Eastern Towhee	*Pipilo erythrophthalmus*	x	x	x	x	x	x	x	x	x	x	x
Field Sparrow	*Spizella pusilla*		x			x	x		x			
Song Sparrow	*Melospiza melodia*		x			x	x		x		x	
Scarlet Tanager	*Piranga olivacea*	x				x			x			x
Northern Cardinal	*Cardinalis cardinalis*			x	x					x	x	x
Rose-breasted Grosbeak	*Pheucticus ludovicianus*		x					x	x			x
Indigo Bunting	*Passerina cyanea*				x		x	x		x		
Red-winged Blackbird	*Agelaius phoeniceus*									x		
Brown-headed Cowbird	*Molothrus ater*									x		
American Goldfinch	*Spinus tristis*	x	x			x	x	x	x	x	x	x



Appendix B. Map showing locations of study sites and bird surveys as described in Appendix A. Sites included in this study are circled. Surveys were not conducted at the BC or CO sites, as those sites were added after federal and state agency staff notified me that GWWA were present there.